Fate of juvenile salmonids stranded in off-channel pools: implications for nutrient transfers

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RESEARCH ARTICLE

Fate of juvenile salmonids stranded in off-channel pools: implications for nutrient transfers

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Abstract

Fish stranding is a complex phenomenon largely attributed to anthropogenic causes in regulated rivers. Although our knowledge of the frequency of stranding and fate of stranded fish in unregulated rivers is limited, this phenomenon may be widespread and important for the transfer of nutrients from aquatic to terrestrial ecosystems. Using a combination of observational data, an experimental manipulation, and a nitrogen subsidy model, we investigated the fate and implications of fish stranded in off-channel pools created by the last spring flood, in the Kadashan River watershed on Chichagof Island, Alaska, USA. Of fish stranded in pools (exclusively juvenile Dolly Varden Char [*Salvelinus malma*] and Coho Salmon [*Oncorhynchus kisutch*]), smaller individuals (age-0; < 74 mm) were more common than larger ones (age-1; > 74 mm). Mortality rate was mainly influenced by cover availability, and larger fish tended to disappear at a higher rate than smaller ones. These observations, together with detection of predator activity, suggest that predation was the main cause of mortality for stranded fish. We estimate that fish stranding occurred during 66% of the years between 1980 and 2015, and that in a single stranding event approximately 1.62 kg of nitrogen is available to predators in the 0.24 km^2 floodplain of the Kadashan watershed surveyed. Thus, fish stranding likely has implications for cross ecosystem connectivity via aquatic nutrient transfers to terrestrial food webs. With projected increases in extreme precipitation and flood events in Southeast Alaska the incidence of fish stranding in unregulated rivers will likely increase. Our results suggest by ensuring that cover (e.g. large wood and artificial structures) is available in off-channel habitats to benefit species or populations of conservation concern.

Keywords Fish stranding · Off-channel pools · Fish mortality · Predation · Drying · Alaska

Introduction

Fish stranding is a complex phenomenon arising from various natural and anthropogenic drivers. Floods, droughts, hydropower operations, and crop irrigation can lead to stark fluctuations of water levels in rivers, resulting in stranding. Research regarding the causes and consequences of fish stranding in freshwater ecosystems is limited, but reported

causes are overwhelmingly anthropogenic in origin (95 of 116 papers; 81%; Nagrodski et al. 2012). Due to a paucity of empirical evidence on fish stranding in unregulated rivers, a better understanding of the mechanisms contributing to their fate is needed. Further, elucidating the causes and consequences of fish stranding is necessary for effectively managing populations of economically and recreationally valuable fishes, especially considering projected alterations to freshwater ecosystems due to climate change (Nadeau and Rains 2007; Lawrence et al. 2010) and human uses of water resources (Kreutzweiser et al. 2013; Cott et al. 2015).

Increased intermittency, and reductions in longitudinal and lateral surface-water connectivity, will likely amplify stranding and lead to fish losses. For example, rapid fluctuations in downstream flows from hydropower activity have resulted in stranding of large numbers of aquatic organisms (Cushman 1985), and increased mortality of juvenile salmonids (Saltveit et al. 2001). Hvidsten and Trout (1985) reported high mortality of stranded Atlantic Salmon (*Salmo*

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salar) and Brown Trout (*S. trutta*) in the regulated Nidelva River, Norway, due to pool drying. Alternatively, the fate of stranded fish would depend on their survival until there is reconnection to main waterbodies by surface flows (Schlosser 1995; Labbe and Fausch 2000; Magoulick and Kobza 2003; Hodges and Magoulick 2011). Indeed, the quality of refugia can have important implications for the fate of stranded fish (Hodges and Magoulick 2011). Isolated habitats that lack cover and available refugia will likely lead to lowered survival of stranded fishes. Howells (1978) found that the main source of mortality for most *Tilapia* spp. stranded in pools following a freak flood in Mandavu Dam, Wankie National Park, Zimbabwe, was predation by large birds.

Floodplain and intermittent river ecosystems are particularly prone to fish stranding (Brown et al. 2001; May and Lee 2004; Leigh et al. 2015), where droughts and floods tend to congregate fish in deep pools within the main channel (i.e., lower velocity), as well as in off-channel habitats and beaver ponds (Bryant 1984; Thedinga et al. 1988; Murphy et al. 1989; Hodges and Magoulick 2011). When water recedes after flooding, many off-channel pools become disconnected from the main channel, leaving fish stranded (Kroger 1973; Hvidsten and Trout 1985; Hesthagen and Hegge 1992). Rivers and streams in southeastern Alaska are characterized by annual flash floods that are short in duration (usually last less than 24 h), and occur approximately 6–12 times a year, mostly in autumn (Pollock 1995). Observations in this region during summer and autumn 1992 suggested that large numbers of fish, mainly juvenile salmonids, become stranded in pools after such floods (M. Ben-David, per. obs). This provided an opportunity to assess the fate of juvenile salmonids stranded in off-channel pools in an unregulated river.

In Southeast Alaska, the predominant juvenile fish predators in freshwater systems are mink (*Neovison vison*), river otter (*Lontra canadensis*), Common Merganser (*Mergus merganser*), and Bald Eagle (*Haliaeetus leucocephalus*; Ben-David 1996; Ben-David et al. 1997). Using a combination of observational data and an experimental manipulation, we assessed the effects of off-channel pool size and availability of cover therein, on the subsequent survival of stranded fish. We hypothesized that fish stranded in pools with cover would experience lower levels of predation than fish stranded in pools without cover. Further, based on predictions from optimal foraging theory (Pyke et al. 1977), we hypothesized that fish size will affect susceptibility to predation. Specifically, larger fish will be more susceptible to predation by terrestrial predators than smaller ones. Finally, we calculated the potential contribution of nitrogen from stranded juvenile salmonids to their terrestrial predators. While adult salmonids represent an essential source of nitrogen to terrestrial ecosystems (Ben-David et al. 1998; Cederholm et al. 1999; Naiman et al. 2002; McLoughlin

et al. 2016), the importance of stranded juveniles, particularly during early summer when subsidies from migrating salmon are not available, remains unknown.
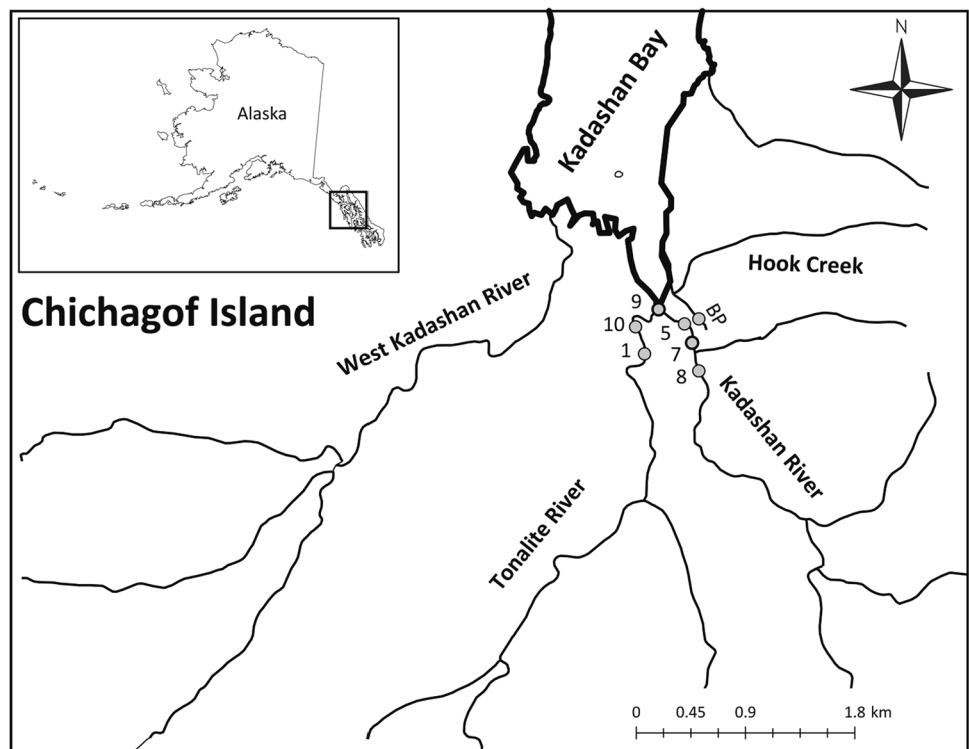
Methods

Study area

This study was conducted in the 0.24 km^2 floodplain of the Kadashan River watershed on Chichagof Island (Fig. 1)—a 5300 km^2 island located in the Alexander Archipelago of the Alaska Panhandle in Southeast Alaska, USA (Tenakee Springs at 57°52′N 135°18′W). The region has a maritime climate; summers are cool and wet and winters are characterized by deep snow (2360 mm annual precipitation). The snow-free period extends from early May to early November. Vegetation at higher elevations is typified by alpine tundra, and at lower elevations by coastal, old-growth rain forest of Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*), with a well-developed understory (mainly *Oplopanax horridus, Vaccinium* spp., *Menziesia ferruginea*, and *Rubus* spp.). The 4th order Kadashan River watershed supports annual runs of spawning Pink (*Oncorhynchus gorbuscha*), Chum (*O. keta*), Coho Salmon (*O. kisutch*), and Stealhead (*Oncorhynchus mykiss*), as well as a summer run of Dolly Varden Char (*Salvelinus malma*). Two additional fish species are common in the Kadashan River watershed: Coastrange Sculpin (*Cottus aleuticus*) and Three-spined Stickleback (*Gasterosteus aculeatus*).

Fish sampling

This undergraduate research project was done concomitantly with a study focused on quantifying the benefits of spawning Pacific Salmon to terrestrial predators and riparian ecosystems in Southeast Alaska (Ben-David et al. 1997, 1998). We sampled six off-channel pools created by the last spring flood (June 15, 1993) above the confluence of the main fork of the Kadashan River and its Tonalite tributary, from the last week of June to early July 1993. All pools were between 1.5 and 3.0 km from the estuary and above tidal influence. The summer of 1993 was exceptionally dry (21.3 mm from June 15–July 15, 1993; 1981–2010 average for the period 88.6 mm; http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?ak9121), and no floods occurred until late July. This resulted in complete drying of beaver ponds in the watershed. Therefore, in addition to the six off-channel pools, we monitored one drying beaver pond, 300 m downstream on the east side of the watershed (Fig. 1). Substrate in all pools ranged from silt to small gravel (< 256 mm diameter). We measured the length (longest axis) and width (shortest axis) as well as depth at the deepest point for each

Fig. 1 Map of the main stream and off-channel pools of the Kadashan River watershed on Chichagof Island, southeast Alaska

Experimental manipulation

To test the hypothesis that large fish will disappear at a higher rate than smaller ones, and because not all pools stranded large individuals, we added fish to four of the flood pools. After counting and classifying the fish already stranded in these four pools, we stocked them with additional fish collected from the river. Stocking was done such that the size distribution in the pools matched that of the river (Ben-David et al. 1997). The numbers and size distribution of fish added to the four pools in the experimental manipulation are described in Table 1.

Monitoring predator activity

Predator activity was monitored by observing tracks in the mud around the pools, direct observations while checking mink and marten (*Martes americana*) traplines (7 km along the Kadashan River watershed; Ben-David et al. 1997), and by photo-trapping. A small camera (Olympus XA2), mounted with a copper-wire trigger and tied to a bait (i.e., dead juvenile salmonid) with a monofilament fishing line, was mounted on a tree adjacent to one of the pools. Using these methods, we identified mink, river otter, mergansers, and bald eagles as the predators.

pool to the nearest cm. Pools with more than 20% of the surface area covered by rocks or large wood were considered protected those.

In pools, fish were collected using backpack electrofishing (Smith-Root Model VII, Vancouver, WA). We verified that all fish were collected from pools without cover by visually observing them after electrofishing. In pools with cover, we had difficulty collecting all the stunned fish, which explains the higher count of fish in the third sampling event compared with the second in pool No. 8 (see results). Individuals were identified to species, measured to the nearest mm (fork length), and returned to the pools. For comparison, we collected fish in the main stem of the Kadashan and Tonalite Rivers in our companion study (Ben-David et al. 1997) using small-mesh (2×2 mm) minnow traps baited with salmon eggs. To compare the proportion of fish captured in the river to that of fish stranding in off-channel pools, we recorded the number of fish captured via baited minnow traps and calculated their proportions. We grouped fish into size-classes based on a length-frequency histogram generated for the in-stream fish (Age 0: 30–41 mm, Age 1: 42–61 mm, Age 2: 62–74 mm, Age 2+: > 74 mm; Ben-David 1996). Because such grouping resulted in small sample sizes, we pooled data for all fish < 74 mm (hereafter "small fish") and fish > 74 mm (hereafter "large fish"). This pooling likely created a species bias because most small fish were Coho Salmon and most large fish were Dolly Varden Char. We monitored pools 3–6 times over the course of the study period (July 7 to 17, 1993).

Table 1 Characteristics and fate of disconnected off-channel pools, a drying beaver pond, and fish collected in the Kadashan River watershed, Chichagof Island, Southeast Alaska, following a flood on June 15, 1993

Pool no.	Pool characteristics				Number and lengths (mm)					Fate
	Length (cm)	Width (cm)	Depth (cm)	Cover	Dolly Varden		Coho Salmon		Sticklebacks	
					< 74	> 74	< 74	> 74		
01	50	100	11	No	0 (2)	0 (10)	11 (23)	0 (5)	0	Dried
05	900	500	41	Yes	0 (1)	0 (5)	10 (14)	2 (9)	0	Unchanged
07	100	300	58	No	9 (2)	0 (3)	21 (14)	0 (9)	0	Dried
08	50	50	22	Yes	0	0	58	0	0	Unchanged
09	600	200	11	No	0 (0)	0 (26)	599 (7)	0 (16)	0	Re-flooded
10	50	80	3	No	0	0	49	0	0	Dried
Beaver pond*	400	100	10	No	26	53	147	68	115	Dried

Raw fish numbers represent the size distribution and abundance of fish captured in each pool following the June flood and prior to the experimental manipulation. Values in parentheses represent the size distribution and number of fish that were trapped in the Kadashan River watershed and stocked in pools on July 6, 1993

*Size at sampling reflects drying

Estimating stranding events

We obtained daily values of precipitation for the study area from 1980 to 2015 using modeled values extrapolated from DAYMET at a 1 km resolution (Thornton et al. 2016). We calculated the mean daily precipitation from all pixels within the study area. We then derived the daily cumulative precipitation from May 1 to August 16 of each year. To estimate stranding events, we first identified flood events based on the slope of the curve during the 20-day flood period prior to fish stranding in 1993. Stranding events were estimated to occur when cumulative precipitation was greater than or equal to 3.9 mm day^{-1}, followed by 10 consecutive days with no additional precipitation.

This is a conservative estimate for stranding in this system (M. Ben-David, per. obs).

Estimating nitrogen availability

For comparison with studies investigating aquatic subsidies to terrestrial ecosystems, we estimated the amount of nitrogen (N) contained in fish stranded in off-channel pools. Percent N was measured for a subset of juvenile Coho Salmon and Dolly Varden Char captured in the river in 1993 (see Ben-David et al. 1997, 1998 for analytical methods). Percent N was similar for size classes and species; therefore, we used an average value in all calculations. Using length-weight relationships, we then estimated biomass of fish naturally stranded in off-channel pools using the average biomass of fish per species per pool. Fish biomass was then converted to grams of N by multiplying average biomass and percent N. To assess the overall N availability in the watershed from stranded fish, we used Google Earth imagery and personal observations (M. Ben-David) from repeated sampling of a 7-km predator trapline to estimate the number of off-channel pools in the Kadashan and Tonalite Rivers during years when stranding occurred.

Statistical analysis

We used a χ^2 test to determine whether fish sizes were different between the river main stem and the isolated pools, as well as whether the number of stranded Dolly Varden Char matched their occurrence in the river, (Zar 2016). We calculated instantaneous mortality rate for small and large fish by log transforming the number of fish in each category remaining in the pool at each sampling, and performing a linear regression on the transformed data. We tested whether cover affected mortality of small fish using ANCOVA with the log-transformed number of fish as the response variable and cover as the predictor variable (Neter et al. 1990). We repeated the same analysis solely for Coho Salmon to decipher species versus size effects. We used Spearmans' rank correlation to determine whether pool volume affected mortality rate of small fish (Zar 2016). We were unable to perform the same analysis for large fish, because one of the stocked pools (No. 9) flooded 2 days after our stocking (high tidal surge elevated river levels) and the surviving fish escaped. Excluding data from this pool left only three pools with large fish which was too small of a sample size for such analysis. All analyses were performed in Program R (R Core Team 2016).

Results

In the river, we captured seven fish species in baited minnow traps; Coho Salmon (46%), Dolly Varden Char (24%), Coastrange Sculpin (14%), Three-spined Stickleback (8%),

Pink Salmon (4%), Chum Salmon (2%), and Stealhead (2%). Of the five species of fish that rear in the river, only juvenile Dolly Varden Char and Coho Salmon were found in flooded pools (Table 1). These two species were most common in the river (Table 1); however, the proportion of Dolly Varden Char in pools was significantly lower than in the river (χ^2 test, $P < 0.001$). In the beaver pond, we found Three-spined Stickleback in addition to Coho Salmon and Dolly Varden Char (Table 1). In the flood pools and beaver pond, majority of the stranded fish were small juvenile salmonids (< 74 mm; Table 1). Similarly, small fish were more common in the river than large fish (χ^2 test, $P < 0.001$). Small fish stranded in pools with cover had lower instantaneous mortality rates than small fish in pools without cover (Fig. 2; ANCOVA, $P < 0.001$). The same result was obtained when the analysis was performed for small Coho Salmon only.

Our analysis indicated a non-significant negative relationship between pool volume and mortality rate (Table 1; Fig. 2; Spearman's rank correlation, $r = -0.5$; $P = 0.391$), probably due to small sample size. In pools lacking cover, the rate of disappearance of larger fish was higher than that of smaller fish (Fig. 2; ANCOVA, $P = 0.03$). Repeating the

analysis for Coho Salmon only suggested a similar trend, but the relationship was not significant (ANCOVA, $P = 0.09$). Of the 409 fishes stranded in the drying beaver pond, only 10 Three-spined Sticklebacks survived 2 days after our initial sampling (Table 1); these individuals were found dead in the dried pool 6 days later.

The most common terrestrial predator detected in all pools was mink (Table 2). On two occasions, we were able to obtain a photograph of a mink feeding in one of the pools (No. 7). Mergansers were observed infrequently, mainly a hen and her ducklings at two pools directly adjacent to the river (No. 1, 7). River otter tracks were observed in two pools and in the drying beaver pond. Bald eagle tracks were observed in only the shallowest pool (No. 10) and a bald eagle was observed walking in the pool after it dried (Table 2). We were unable to document a temporal relation between the occurrence of predator signs and the disappearance of fish because we did not sample pools daily and predator tracks remained in the mud for several days. Nonetheless, predator tracks were abundant in the drying beaver pond following the disappearance of 399 fish of all species and sizes.

Analysis of cumulative precipitation extrapolated from DAYMET suggests that at least one stranding event occurred in 66% of the years between 1980 and 2015, and more than one stranding event occurred in 11% of the years during the same period. Average daily precipitation from 1980 to 2015 was variable, with no consistent temporal frequency of stranding conditions (Fig. 3). Such stranding likely occurred in approximately 38 off-channel pools that form along the Kadashan and Tonalite Rivers. Average biomass of stranded juvenile Coho Salmon (3.35 ± 6.65 g) was much lower
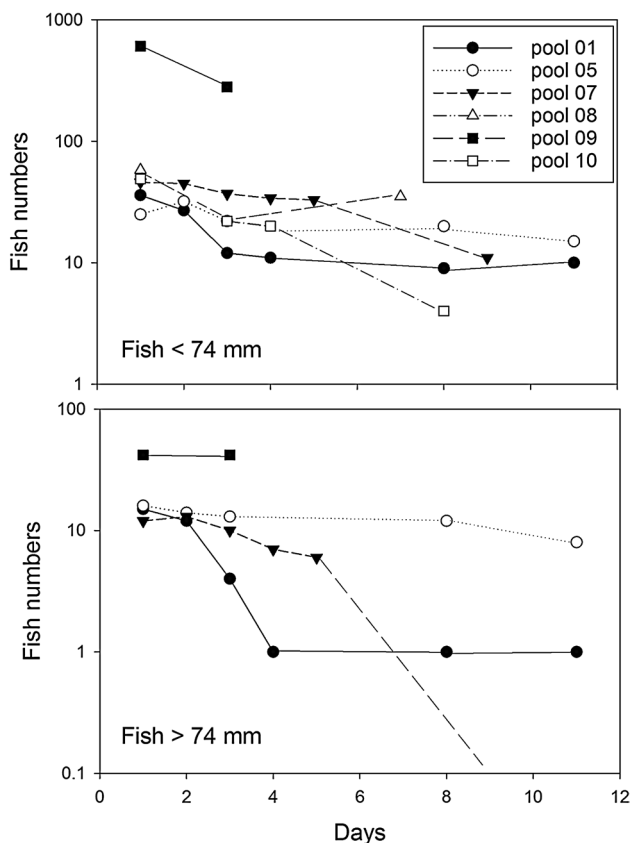

Fig. 2 Mortality rate of small (< 74 mm; top panel) and large (> 74 mm; bottom panel) fish stranded in off-channel pools in the Kadashan River watershed, Chichagof Island, southeast Alaska, July 7 to 17 1993. Fish numbers are plotted on a logarithmic scale

Table 2 Predator tracks (+), direct observations (++), and photographs (p) recorded at flood pools in the Kadashan River, Chichagof Island, southeast Alaska during July 1993

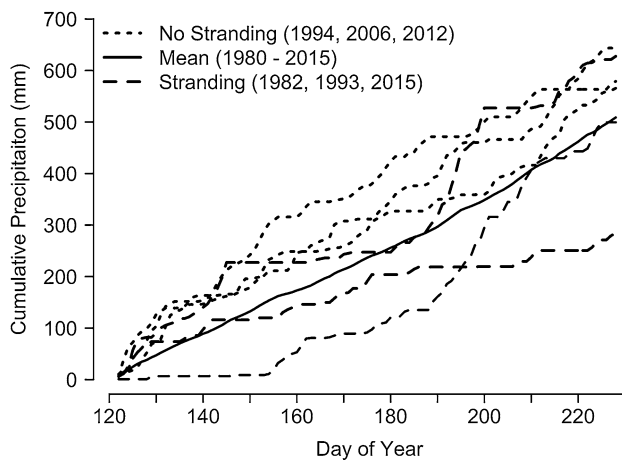| Pool no.	Date	Predator			Bald eagle
		Mink	Otter	Merganser	
1	5-Jul	−	−	−	−
	6-Jul	+	−	−	−
	8-Jul	−	−	++	−
	17-Jul	+	+	−	−
5	8-Jul	+	+	−	−
7	12-Jul	+	−	+	−
	14-Jul	p	−	−	−
	15-Jul	+	−	−	−
	16-Jul	p	−	−	−
	17-Jul	+	−	−	−
10	13-Jul	+	−	−	+
	17-Jul	−	−	−	++
Beaver	1-Jul	+	+	−	−

Fig. 3 Cumulative precipitation from May 1 to August 16 in the Kadashan River watershed. Examples of 3 years (1993, 2004, and 2015) when stranding events occurred, 3 years (1994, 2006, 2012) when standing did not occur, and mean cumulative daily precipitation from 1980 to 2015. Stranding events were estimated to occur when cumulative precipitation was greater than or equal to 3.9 mm day^{-1}, followed by 10 consecutive days with no additional precipitation

Fig. 4 Length-weight relationship and percent nitrogen values for Dolly Varden Char and Coho Salmon collected in the Kadashan River watershed, 1993

than the average biomass of juvenile Dolly Varden Char (9.53 ± 10.11 g). On average 55 g of juvenile Coho Salmon and 5 g of Dolly Varden Char were stranded in off-channel pools in the Kadashan River watershed in 1993. Percent N was similar for both species, averaging 11.6 and 11.2% for Coho Salmon and Dolly Varden Char, respectively (Fig. 4). With approximately 71% of the off-channel pools lacking meaningful cover to provide refugia to stranded salmonids, we estimate that approximately 1.62 kg of N would be available to terrestrial predators in a single stranding event in the Kadashan watershed.

Discussion

Our study suggests that predation was the main factor influencing short-term survival of stranded juvenile Dolly Varden Char and Coho Salmon in an unregulated river in Southeast Alaska. Although fish size influenced susceptibility to stranding, we observed fewer than expected Dolly Varden Char trapped in pools, which may suggest species-specific vulnerability. After stranding, cover in the form of rock overhangs and large wood provided protection from predation. Larger fish were more susceptible than smaller fish as predicted by optimal foraging theory. Nonetheless, complete drying of pools would eliminate the chance of survival for stranded fish even without predation. With increases in the frequency of extreme precipitation and flooding events in Southeast Alaska, and elsewhere due to climate change (Dore 2005; Woodward et al. 2010; IPCC 2014), it is likely that the incidence of fish stranding in unregulated rivers will
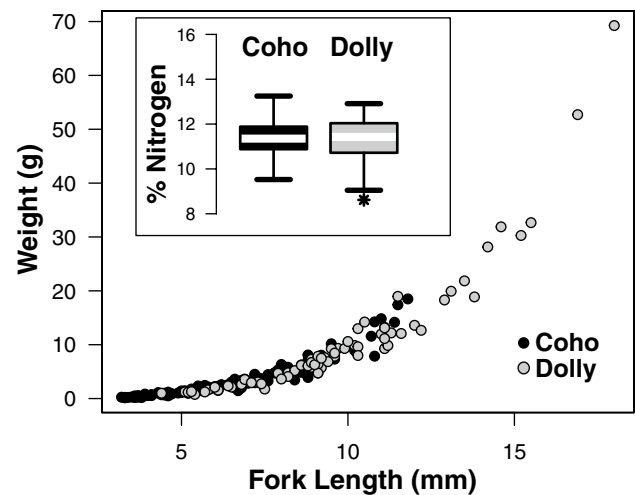
increase. Our results suggest that in preparation for such a future, managers should ensure that cover in the form of large wood or artificial structures is available in channels off the main stem to benefit species or populations of conservation concern. These structures would provide enhanced refugia for fish during flooding and subsequent stranding by buffering predation and increasing survival of stranded fish.

Three points of evidence suggest that predation was the main cause of mortality for stranded fish: (1) in pools with cover, mortality rate was significantly lower for small fish, irrespective of pool size; (2) larger fish tended to disappear at a faster rate than smaller fish; and (3) our direct observations and photo-trapping indicated that predator activity was common and corresponded with fish disappearance. Dollof (1993) argued, based on numbers and sizes of otoliths in feces of otters, that predation by these mustelids comprised a large proportion of the annual mortality of juvenile salmonids in Southeast Alaska. It is unclear whether predation on juvenile salmonids at the rate we observed is limited to dry years or occurs on a regular basis. The Dollof (1993) study was conducted in 1985 which was also characterized by stranding conditions, and in which many beaver ponds in the Kadashan watershed completely dried. Thus, if large numbers of juvenile salmonids become stranded in off-channel pools, drying out of pools (4 of 7 pools in our study) will eliminate the chance of survival even without predation.

We found that smaller fish were more common in our study pools than larger fish. Similar results were obtained in the Nidelva River (Norway) where most of the stranded fish, following a decrease in water-levels in the river, were age-0 (Hvidsten and Trout 1985). Hesthagen and Hegge (1992) also reported that a larger number of pond-reared Brown Trout, which were significantly smaller than hatchery-reared

fish, were stranded in their experimental pond. We offer three possible hypotheses to explain our observations: (1) small fish are less able to withstand main channel velocities during floods, and therefore will seek off-channel pools more often (Bryant 1984; Sullivan et al. 1987; Dollof and Reeves 1990; Hughes and Dill 1990); (2) small fish are more abundant in the main stem of the river, and therefore have a higher likelihood of getting stranded in pools (Murphy et al. 1984; Ben-David 1996); (3) larger fish disappear at a faster rate than smaller ones. For example, because our initial sampling occurred more than 2 weeks after the last spring flood, the actual size distribution of fish at the time of stranding may have been skewed towards larger fish than what we recorded.

In addition to effects of fish size, the two salmonids showed different susceptibilities to stranding. One explanation for differential susceptibility to stranding could be body shape and swimming performance. Taylor and McPhail (1985) found differences in swimming abilities between populations of Coho Salmon, with coastal populations exhibiting deeper, more robust bodies compared to the more fusiform bodies of inland populations. Coastal populations also had lower swimming stamina and greater burst speeds than their inland counterparts. Several studies have shown that juvenile Coho Salmon move into off-channel pools throughout much of the year (Swales et al. 1986; Swales and Levings 1989), these authors attributing the use of off-channel pools to an avoidance strategy for high main-channel flows. Swales and Levings (1989) deemed off-channel pools in British Columbia as important rearing habitat for juvenile Coho Salmon because stranded fish had faster growth rates compared to main-channel fish. However, the susceptibility, use, and fate of fish in off-channel and refuge habitats are highly context dependent. For example, in two different intermittent Ozark streams, researchers have found that four species of Cyprinids exhibit differential responses in movement, survival, and abundance related to refuge habitats. These appear to be related to species-specific life histories and attributes of the local environment (Hodges and Magoulick 2011; Walker et al. 2012; Walker and Adams 2014). If, as projected, rivers become more intermittent and flashy due to impacts of climate change and human development, susceptibility of fishes to stranding will likely also increase, but stranding rate will depend on the focal species and their life histories. Therefore, further examination of species vulnerability to stranding is needed to better understand this complex phenomenon.

Mortality of smaller fish was largely influenced by availability of cover, regardless of whether the analysis was performed on the pooled data or solely for Coho Salmon. Several other studies have emphasized the importance of cover for fish, mainly as protection from predation (Oswood and Barber 1982; Hunter 1991; Murphy and Meehan 1991).

Food availability and oxygenation, which could affect survival of stranded fish, seem to be less important in our case. We did not find a significant relationship between pool size and mortality rate of small fish. It is possible that pool size may become an important factor if fish were to survive in them longer as availability of food would become limiting. Also, because fish survived in these small pools for over 2 weeks before our initial sampling, and some survived during our experiment, it is likely that the pools were receiving sufficient oxygen either through atmospheric diffusion or through oxygenated hyporheic flow. In fact, one of the pools (No. 8) was located on a gravel bar of the braided river channel which lacked surface connectivity, but had steady hyporheic flow (M. Ben-David, per. obs).

Finally, while the ecological benefits of adult spawning salmonids to terrestrial ecosystems are largely known (Naiman and Decamps 1997; Ben-David et al. 1998; Naiman et al. 2002), the benefits of stranded juvenile fish as a food and nutrient resource have been mostly ignored. Several studies from Alaskan rivers have documented that a variety of terrestrial predators including mink, marten (*Martes americana*), river otters, Common Mergansers, Great Blue Herons (*Ardea herodias*), and Bald Eagles often feed on stranded fishes in side-channels, off-channel pools, and beaver ponds during periods when other food sources are limited (Alexander 1979; Wood 1987; Nagrodski et al. 2012). For example, Dollof (1993) estimated that at least 3300 juvenile Coho Salmon and Dolly Varden Char were consumed by two river otters in the Kadashan River in 1985 over the 6-week study period. Based on our measures, we can conservatively estimate that these two individuals in Dollof's (1993) study acquired 2.4 kg of N from juvenile salmonids in early summer. Obviously, these and the quantities we calculated for stranding events are approximately 4900 times lower than the input of N to terrestrial predators from adult salmon per year (i.e., 8000 kg of N in the Kadashan River; Gende et al. 2002; Willson et al. 2004). They are also likely lower than those derived from summer emerging aquatic insects. For instance, studies from Costa Rica, Arizona, Kansas, and North Carolina suggest that emergence of aquatic insects is responsible for the transfer of 0.825–4.25 mg of N m^{-2} day^{-1} from streams to the surrounding terrestrial landscape (Grimm 1987; Gray 1989; Small et al. 2013). Assuming maximal rates (i.e., 4.25 mg N m^{-2} day^{-1} from July 1 to August 16) for the Kadashan and Tonalite Rivers results in approximately 47.7 kg N each summer, or 29.4 times higher than our stranding estimates. Nonetheless, we suggest that it is the timing of stranding that is important to terrestrial predators, as these usually occur prior to the arrival of spawning adults and insect emergence. In late-spring and early summer, juvenile salmonids can provide an important food and N source to predators engaged in the costly effort of rearing young (Ben-David et al. 1997).

Considering projected alterations to freshwater ecosystems from climate change and a paucity of data regarding natural fish stranding, assessing the role of stranded fish in aquatic subsidies to terrestrial food webs would be a fruitful line of inquiry.

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